

# Plant community establishment following drawdown of a reservoir in southern Arkansas, USA

Rebecca J. Howard · Christopher J. Wells

Received: 22 April 2008 / Accepted: 13 February 2009  
© Springer Science+Business Media B.V. 2009

**Abstract** Wetland area, function and wildlife habitat value are extensively altered by the construction of freshwater reservoirs. We studied the effects of a temporary drawdown on shoreline vegetation communities of Felsenthal Navigation Pool (“the pool”), an impoundment at Felsenthal National Wildlife Refuge in southern Arkansas that is managed as a greentree reservoir. The pool was permanently flooded from 1985 until the summer of 1995 when the water level was dropped 0.3 m for about 16 weeks, exposing about 1,591 ha of soil. To document plant succession on the sediments exposed, we recorded plant species composition and cover at 14 transects along the pool margin prior to the drawdown, during the drawdown, and in the following summer. A soil disturbance treatment was applied near five transects following the drawdown, and soil was collected at each transect for seed bank and soil analyses. Plants colonized the drawdown zone quickly and high vegetation cover was present at some transects 4 weeks after the drawdown was initiated. Plants included species that are high quality food sources for waterfowl, including *Cyperus erythrorhizos* and *Leptochloa fascicularis* var. *fascicularis*. Vegetation response, measured by species

richness, total cover, and cover of *Cyperus* species, was often greater at low compared to high elevations in the drawdown zone; this effect was probably intensified by low summer rainfall. Response on the disturbed transects was lower than that on the undisturbed transects. This effect was attributed to two factors: (1) removal of the existing seed bank by the disturbance applied and (2) reduced incorporation of seeds recruited during the drawdown because of unusually low rainfall. Seed bank studies demonstrated that several species persisted despite 10 years of continual flooding, and that seed bank species richness increased during the drawdown. Although conclusions are limited by the 1-year time frame of the study, it is unlikely that permanent change to plant community structure in the drawdown zone resulted from the lowered water level.

**Keywords** Freshwater wetland · Impoundment · Plant community · Reservoir · Seed bank · Shoreline vegetation · Water level manipulation · Waterfowl food plants

## Introduction

Plant community development on sediments exposed by the receding waters of permanent freshwater lakes and reservoirs has received limited study. This has been attributed to the fact that such drawdowns are

R. J. Howard (✉) · C. J. Wells  
US Geological Survey, National Wetlands Research  
Center, 700 Cajundome Boulevard, Lafayette,  
LA 70506, USA  
e-mail: howardr@usgs.gov

often unpredictable and relatively infrequent, requiring extreme drought or anthropogenic manipulations (DeBerry and Perry 2005). Seeds prevented from germinating in flooded conditions may germinate when mudflats along shorelines are exposed at anytime during the growing season (Baskin et al. 1993), providing a potential food source for wildlife. Plant food quality and quantity are influenced by several factors, including available seed source, seed bank composition, seed germination conditions, and plant growth and survival. Land managers in the lower Mississippi River Valley of the south-central United States use various techniques to influence plant succession and species composition in wetlands, including water level manipulation, prescribed fire, soil treatments such as disking, and vegetation plantings, with the intent to increase habitat quality for various invertebrate and vertebrate species. These activities demonstrate recognition of the importance of disturbance regimes in affecting wetland plant community structure and function and in influencing biodiversity in wetland systems. Two management techniques widely used by land managers to improve habitat quality for waterfowl include constructing greentree reservoirs in forested areas and seasonally flooding herbaceous habitats, a practice called moist-soil management.

Greentree reservoirs (GTRs) are created by impounding bottomland forest habitat during the dormant season to increase food availability for migrating and wintering waterfowl (Fredrickson and Batema 1992). Early reports on the effects of GTRs indicated either no impacts or positive impacts of the flooding regime on tree health and mast production (Broadfoot 1958; Merz and Brakhage 1964; Broadfoot 1967). Later studies, however, demonstrated long-term negative impacts of GTR management on forest composition and structure (Malecki et al. 1983; Young et al. 1995; King and Allen 1996; King et al. 1998; Fredrickson 2005; Gray and Kaminski 2005; Ervin et al. 2006), including a shift to more flood-tolerant species and reduced woody species regeneration. Moist-soil management practices involve manipulating water depth and flooding duration and seasonality within impoundments to stimulate growth of herbaceous plants from seeds or tubers present in the soil, thereby maximizing food production (Reineke et al.

1989). Several factors influence the resulting vegetation community on moist-soil units, including timing of the drawdown, seed or propagule availability, soil type, soil temperature, soil salinity, litter, and soil moisture level (Fredrickson 1991; Brock et al. 1994). Direct soil manipulation such as disking and tilling has also been used in moist-soil management to influence plant community composition and structure (Fredrickson and Taylor 1982; Fredrickson and Reid 1988; Gray et al. 1999). However, a host of abiotic and biotic factors that affect seed germination and propagule success make it difficult to predict the outcome of moist-soil management practices. The correlation between composition of seed banks and standing vegetation often varies among sites within a wetland (Leck 1989; Rossell and Wells 1999) and over time (Leck and Simpson 1995). Predictions are further complicated by the fact that hydrologic history can also influence the composition of the seed bank and seed viability. Seed bank species richness was found to decrease with increasing water depth in freshwater marshes (Wilson et al. 1993) and with longer duration of flooding in intermittent freshwater wetlands (Casanova and Brock 2000). Few viable seeds of emergent plants were found in sediments from a Texas reservoir following several years of inundation (van der Valk and Pederson 1989); Schneider and Sharitz (1986) also noted that continuous flooding decreased seed incorporation into forested wetland seed banks.

We studied plant establishment on soils exposed during an experimental drawdown of a large constructed reservoir that had been continuously flooded for nearly a decade. We hypothesized that the low number of emergent species represented in the standing vegetation before the drawdown would lead to low species richness in both the post-drawdown standing crop and seed bank species richness, and that soil disturbance would act to increase species richness. Specific objectives were to (1) describe plant community establishment within the zone exposed by the reduced water depth, (2) determine the influence of relative elevation on plant community composition, (3) compare post-drawdown vegetation to the species composition of the available seed bank, and (4) quantify the effect of soil disturbance on plant community composition and structure.

## Methods

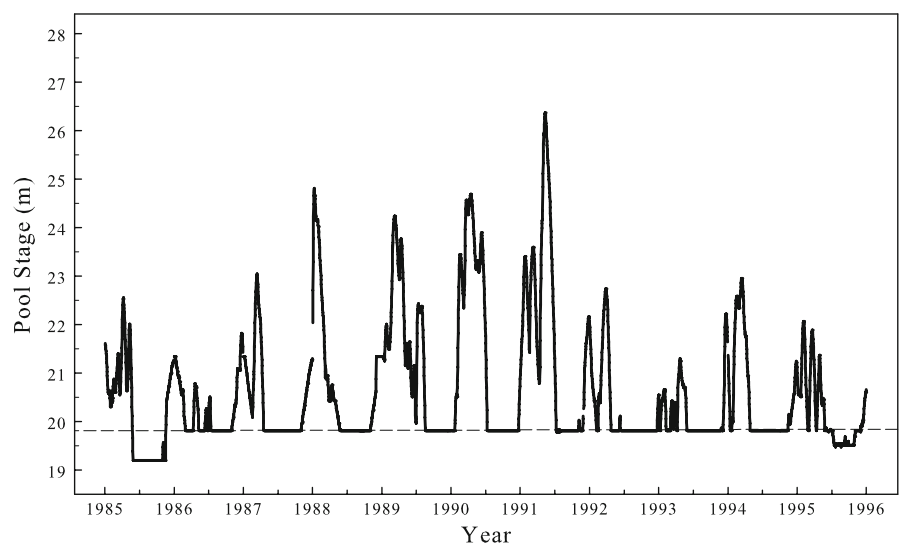
### Study area and experimental design

Felsenthal National Wildlife Refuge (NWR) (33°05' N; 92°08' W) in southern Arkansas is part of a national system of public lands managed by the US Fish and Wildlife Service for the purpose of conserving natural resources. It was established in 1975 to partially mitigate impacts of the US Army Corps of Engineers' (USACE) Ouachita-Black Rivers Navigation Project on bottomland forest habitat. The navigation project included construction of Felsenthal lock and dam in 1985, which, in combination with an earlier-constructed dam, resulted in flooding of refuge lands below 19.8 m mean sea level (msl). Approximately 6,450 ha of bottomland forest habitat were permanently flooded by the resulting reservoir (King et al. 1998). The reservoir, Felsenthal Navigation Pool (hereafter "the pool", also known as Lake Jack Lee), is managed by the USACE as a GTR. Under the GTR management schedule, the pool was continuously flooded to at least 19.8 m msl from November 1985 until the summer of 1995 (Fig. 1). On 5 July 1995, the USACE initiated a partial drawdown of the pool to reduce the water level by about 0.3 m. The target drawdown water level at 19.5 m msl was reached on 15 July 1995, exposing about 1,591 ha of previously flooded soil (geographic information system [GIS] analysis conducted by the US Geological Survey National Wetlands Research

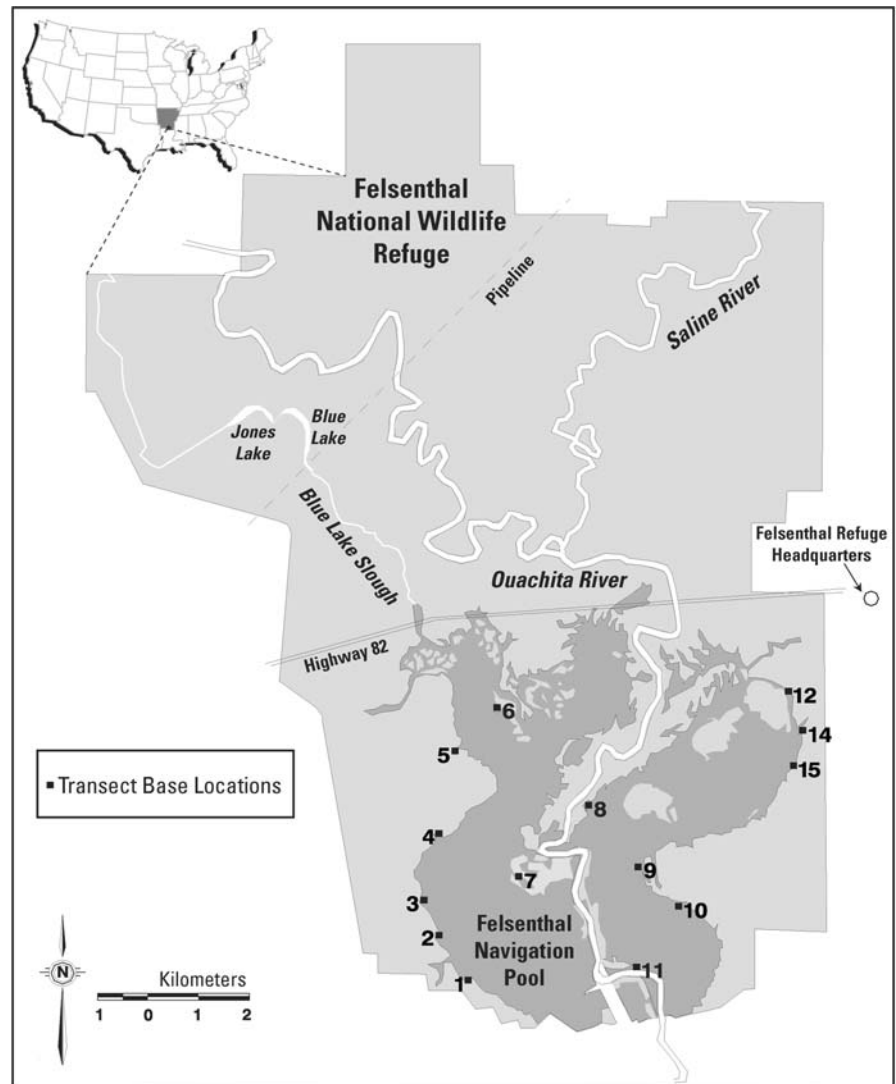
Center, Lafayette, Louisiana). Water level in the pool remained at the drawdown level for over 3 months and was raised beginning 25 October 1995; the pool base water level of 19.8 m was reached on 5 November of that year.

Plant community composition and structure and soil characteristics were monitored prior to the drawdown along 14 permanent transects (Fig. 2) that were selected by refuge staff as characteristic of the pool margin. The base of each transect was located at the pool edge prior to the drawdown event (reference elevation 19.8 m msl), and transects extended perpendicular from the pool margin into the pool to end at 19.5 m in elevation. Global Positioning System (GPS) locations (NAD83) were determined for the transect bases; the readings were corrected by using real-time differential and were accurate to <5 m. Permanent 1-m<sup>2</sup> sampling quadrats were located at the pool margin (base station or quadrat 0) for each transect and at decreasing elevation intervals of approximately 6.1 cm. Elevation at each quadrat was measured with a laser level. Six quadrats, with the final quadrat located at about 19.5 m elevation, were initially established for each transect; the horizontal distance between quadrats was recorded. Quadrat elevation was measured again following drawdown; because a liquid soil slurry at the sediment surface consolidated upon drying, post drawdown elevations were often higher than those obtained prior to drawdown. For several transects, a seventh quadrat was added to sample the true lower

**Fig. 1** Mean daily water levels recorded at Felsenthal lock and dam from 1985 to 1996. Pool stage refers to the surface water elevation relative to mean sea level as measured at the Felsenthal lock and dam. Major tic marks on the x axis indicate January 1, and minor tic marks indicate July 1 of each year



**Fig. 2** Map of Felsenthal National Wildlife Refuge showing approximate locations of transects along the perimeter of Felsenthal Navigation Pool



extent of the drawdown. Considering the original pool edge as a relative elevation level of 30 cm and the pool edge during drawdown as 0 cm elevation, quadrat elevations were classified into two categories: high ( $\geq 15.0$  cm) and low ( $< 15.0$  cm).

Following drawdown, soil disturbance treatments were established for five transects that were accessible to heavy equipment. The disturbance consisted of scraping the soil surface with a bulldozer to create a strip about 10-m wide parallel to, and about 20 m to the right of, the original transect. The five paired transects (transects 2, 3, 4, 14, and 15; Fig. 2) were identified by following the transect number designation with the letter “a” for undisturbed transects and the letter “b” for disturbed transects.

#### Data collection

A vegetation survey was conducted prior to the initiation of the pool drawdown, beginning 26 June 1995. Species composition was recorded, and cover class of all species was estimated in each quadrat by using a modified Daubenmire cover scale (Bonham 1989). The six cover classes used, based on percent cover, were: *P*,  $< 1\%$ ; 1, 1–10%; 2, 11–25%; 3, 26–50%; 4, 51–75%; and 5,  $> 75\%$ . A soil core (9-cm diameter by 15-cm deep) was collected outside each quadrat to determine soil organic matter. An additional core was collected outside quadrat 1 (high elevation, about 24 cm) and quadrat 4 (low elevation, about 6 cm) at each transect for seed bank analysis.

A final soil core was collected midtransect, outside quadrat 2 (about 18 cm elevation), for analysis of particle size distribution of the soil mineral fraction. All soil samples were stored on ice in the field and refrigerated upon return to the laboratory until analysis. No initial data were collected for the areas designated as soil disturbance treatments.

Subsequent to pool drawdown, transects with soil disturbance were established near five of the original transects and all 19 transects were sampled at approximately 6-week intervals in August (time 2), September (time 3), and October (time 4) 1995. Plant species composition and cover were measured during all sampling events. In October, soil core samples were collected outside quadrat 0 (30.5 cm elevation) and quadrat 5 (about 0 cm elevation) for seed bank analysis, and outside quadrat 4 (about 6 cm elevation) for determination of organic matter. The soil core used for sample collection was 2 cm in diameter and 15 cm deep; to compensate for the smaller sample size compared to the June soil samples, three cores were taken at each location and combined prior to analyses. Species composition and cover were sampled a final time in June 1996 (time 5) when water was at base level.

Species composition of the seed bank was determined by using the seedling emergence method (Poiani and Johnson 1988). Soil cores were stored about 3 months at 7°C; following cold storage, the samples were mixed with tap water and large plant tissues were removed to prevent regeneration from remnant rhizomes. The resulting slurry was evenly spread over commercial potting soil in standard plastic flats (25.4-cm by 25.4-cm by 5.1-cm deep). The flats were randomly arranged on a plastic-lined table in a greenhouse in Lafayette, Louisiana, and water on the table was maintained at a constant depth of 2 cm by adding tap water. A water-cooling system in the greenhouse kept the maximum temperature below 35°C. Cover class of all seedlings was estimated after 6 weeks; all seedlings were then removed from the trays. Cover was estimated a second time after an additional 8 weeks of growth. The two seed bank experiments were initiated in September 1995 (June samples) and April 1996 (October samples).

Soil cores for physical analyses were dried at 55°C to a constant weight and then homogenized by mixing. Organic matter was determined by applying

loss upon ignition techniques (Soil and Plant Analysis Council 1992). Particle size distribution of the mineral fraction was measured following digestion of organic matter in household bleach. The sand fraction was removed by using wet sieving, and the clay and silt fractions were determined by using the pipette method (Schumacher et al. 1995).

### Statistical analysis

All analyses were conducted by using SAS/STAT® software, Version 6 (SAS Institute, Inc., Cary, North Carolina). A multivariate two-way nested analysis of variance (ANOVA) model was used to analyze vegetation prior to (June 1995, time 1) and following (June 1996, time 5) the drawdown, with transect and elevation class (low or high) within transect as independent variables. The analyses were conducted by using the general linear model procedure (Proc GLM) of SAS software. A significance level of  $\alpha = 0.05$  was used for these and all subsequent analyses; the significance level was adjusted for the number of comparisons when appropriate. When required, variable transformations were made to conform to model assumptions. To determine how vegetation responded during the drawdown (times 2–4), a repeated-measure multivariate ANOVA (MANOVA) model was applied. Disturbed and undisturbed transects were analyzed separately. In all vegetation analyses, the cover class variable for each species was converted to the percentage of cover represented by the midpoint of the class range (e.g., class 2 was converted to 18%); Class P was assigned a cover value of 0.5%. The dependent variables for vegetation analyses were species richness, percentage of total vegetation cover, and percentage of *Cyperus* cover, defined as the sum of *Cyperus iria*, *Cyperus erythrorhizos*, and Cyperaceae (those plants only identified to this family level) cover values. To further investigate the effect of soil elevation, transects were pooled, and a one-way ANOVA was performed by using elevation class as an independent variable. Disturbed and undisturbed transects were again analyzed separately, and repeated measures techniques were applied for times 2–4. The effect of soil disturbance and disturbance by elevation on vegetation for the five transects that included a parallel disturbed transect were examined with paired *t*-tests.

The effect of elevation on seed bank species richness was examined by using a one-way ANOVA with elevation class as the independent variable. Seed bank species richness was compared to that of the standing crop in both June and October by using paired *t*-tests; paired *t*-tests were also conducted to describe the effect of disturbance on seed bank species richness (October samples). Two-way ANOVA was used to examine the effect of transect and elevation on soil organic matter content, and a paired *t*-test was used to examine the effect of disturbance on this variable.

## Results

### Transect and plant community descriptions

Transects varied from 22.0 to 223.6 m in length, and relative elevation of the quadrats in reference to the transect base stations (defined as 30 cm elevation) ranged down to −5.5 cm. Plants quickly colonized undisturbed areas of the drawdown zone. We identified 63 vascular plants and two bryophytes within quadrats (Table 1); 13 of the vascular plants were identified only to genus or family level, and one species was unknown. Species frequency, defined as the percentage of total quadrats (all transects) in which a species was found, ranged from 0 to 89.6% (*Wolffia* sp., June 1996) during the study; mean total cover by species in all quadrats by time ranged from 0 to 26.4% (*Ludwigia peploides*, August 1995). While flooded in June 1995 and 1996, the most frequent species and species with the highest cover were primarily submersed or floating; during the drawdown, emergent species became common (Table 2).

The number of woody plant species, including vines, increased as a result of the pool drawdown. Woody species were absent from the list of five most frequently-occurring species in June and August 1995, but *Cephalanthus occidentalis* was the second most frequently-occurring species in both September and October 1995 (Table 2). In June 1995 just two woody species (*Cephalanthus occidentalis* and *Taxodium distichum*) occurred at a frequency of 19.0% in all quadrats combined. During the drawdown, woody species richness increased to three and seven in

**Table 1** Plant species identified at 19 transects at Felsenthal Navigation Pool, Felsenthal National Wildlife Refuge

Species	Life form
Vascular:	
<i>Ammannia coccinea</i> Rottb.	E
<i>Azolla caroliniana</i> Willd.	F
<i>Bacopa egensis</i> (Poepp.) Pennell	E
<i>Bacopa rotundifolia</i> (Michx.) Wettst.	E
<i>Bidens aristosa</i> (Michx.) Britt.	E
<i>Brunnichia ovata</i> (Walt.) Shinnars	W
<i>Cabomba caroliniana</i> Gray	S
<i>Carex</i> sp.	E
<i>Cephalanthus occidentalis</i> L.	W
<i>Ceratophyllum demersum</i> L.	S
Cyperaceae	E
<i>Cyperus erythrorhizos</i> Muhl.	E
<i>Cyperus iria</i> L.	E
<i>Diodia teres</i> Walt.	E
<i>Diospyros virginiana</i> L.	W
<i>Echinochloa crus-galli</i> (L.) Beauv.	E
<i>Echinodorus cordifolius</i> (L.) Griseb.	E
<i>Eclipta prostrata</i> (L.) L.	E
<i>Eleocharis microcarpa</i> Torr.	E
<i>Eleocharis obtusa</i> (Willd.) J. A. Schultes	E
<i>Fimbristylus miliacea</i> (L.) Vahl	E
<i>Gleditsia aquatica</i> Marsh.	W
<i>Heteranthera reniformis</i> Ruiz & Pavon	E
<i>Hibiscus</i> sp.	E
<i>Hydrolea quadrivalvis</i> Walt.	E
<i>Ipomoea</i> sp.	E
<i>Juncus</i> sp.	E
<i>Leersia oryzoides</i> (L.) Sw.	E
<i>Leptochloa fascicularis</i> (Lam.) Gray	E
<i>Limnobium spongia</i> (Bosc) L. C. Rich. ex Steud.	F
<i>Lindernia dubia</i> (L.) Pennell	E
<i>Ludwigia decurrens</i> Walt.	E
<i>Ludwigia leptocarpa</i> (Nutt.) Hara	E
<i>Ludwigia palustris</i> (L.) Ell.	E
<i>Ludwigia peploides</i> (Kunth) Raven	E
<i>Ludwigia sphaerocarpa</i> Ell.	E
<i>Ludwigia uruguayensis</i> (Camb.) Hara	E
<i>Mikania scandens</i> (L.) Willd.	E
<i>Mimosa strigulosa</i> Torr. & Gray	E
<i>Myriophyllum</i> sp.	S
<i>Najas</i> sp.	S
<i>Panicum</i> sp.	E

**Table 1** continued

Species	Life form
<i>Planera aquatica</i> J. F. Gmel.	W
<i>Pluchea foetida</i> (L.) DC	E
<i>Poa annua</i> L.	E
<i>Poa autumnalis</i> Muhl. ex. Ell.	E
Poaceae	E
<i>Potamogeton</i> sp.	S
<i>Rhynchospora</i> sp.	E
<i>Sagittaria graminea</i> Michx.	E
<i>Sagittaria latifolia</i> Willd.	E
<i>Sagittaria</i> sp.	E
<i>Sesbania exaltata</i> (Raf.) Rydb. ex A. W. Hill	E
<i>Sphenoclea zeylanica</i> Gaertn.	E
<i>Spirodela polyrrhiza</i> (L.) Schleid.	F
<i>Taxodium distichum</i> (L.) L. C. Rich.	W
<i>Triadenum walteri</i> (J. G. Gmel.) Gleason	E
<i>Utricularia gibba</i> L.	S
<i>Utricularia inflata</i> Walt.	S
<i>Vitis rotundifolia</i> Michx.	W
<i>Wolffia</i> sp.	F
<i>Xanthium strumarium</i> L.	E
Bryophytes:	
<i>Riccia</i> sp.	
<i>Ricciocarpos</i> sp.	

Plant names according to the Integrated Taxonomic Information System (2007). Life form designation is E, emergent herbaceous; F, floating-leaved; S, submersed aquatic; W, woody

August and September, respectively, and then dropped to four in October. Woody species frequency was 16.9, 55.6, and 39.2% in August, September, and October, respectively. In June 1996, four woody species were found at a frequency of 20.0%.

Mean species richness was higher during flooded conditions compared to the drawdown at several transects (Fig. 3). Patterns in total cover by transect (Fig. 4) resembled those of species richness. *Cyperus* species cover was very sparse prior to the drawdown, but composed more than 50 percent of total cover in some transects in September and October (Fig. 5); *Cyperus* was absent during sampling in June 1996. Overall means for the three vegetation response measures in the 14 undisturbed transects was greater than means for disturbed transects at all measurement times (Table 3).

### Transect and elevation effects

In June 1995, when the pool was at base level, vegetation response varied by elevation ( $P = 0.0155$ ). Total cover differed by elevation for two of the 14 transects; cover at low elevation was significantly greater than that at high elevation at one transect while the opposite relationship was found at the other. In June 1996, when the pool again was flooded to base level, vegetation response varied by transect at undisturbed sites ( $P = 0.0012$ ). Mean species richness at this time ranged from  $3.2 \pm 0.4$  to  $7.4 \pm 0.6$ , with overlap among transects with intermediate values (Fig. 3). Transect and elevation effects were not significant at disturbed transects.

During the drawdown, transect and the time and elevation interaction significantly affected vegetation response on undisturbed transects; vegetation on the disturbed transects was not affected (Table 4). For the undisturbed transects, there were often overlapping groups of similar mean values by transect for each of the vegetation variables, and no consistent patterns in groupings across time were apparent. Significant elevation effects at a particular time were found in undisturbed transects for total cover in August and for *Cyperus* cover in August and September (data not shown). In August, total cover was greater in the high compared to low elevation class at a single transect; no other significant responses were identified for this variable. Elevation affected *Cyperus* cover in three transects in August and September; in all cases, cover was lesser at high compared to low elevation. Over time, elevation significantly affected richness (two intervals), total cover (three intervals) and *Cyperus* cover (two intervals) on several transects (data not shown). While the results are difficult to present in detail, general patterns were evident. Richness increased from August to September at both elevation classes, but the magnitude of the increase was greater at low compared to high elevations. From September to October, richness decreased at high elevation for four transects, while at low elevation it decreased at three transects and remained steady at the fourth. At two transects where richness decreased over time at both elevations, the magnitude of change was greater at low compared to high elevation. Total cover from August to September increased or remained relatively constant at low elevations, but decreased at high

**Table 2** Five most frequently-occurring species and five species with the highest total cover at five sampling times, listed in decreasing order

Month	Frequency	Total cover
June 1995	<i>Spirodela polyrrhiza</i>	<i>Spirodela polyrrhiza</i>
	<i>Ludwigia palustris</i>	<i>Eleocharis microcarpa</i>
	<i>Limnobium spongia</i>	<i>Najas</i> sp.
	<i>Utricularia gibba</i>	<i>Ludwigia palustris</i>
	<i>Wolffia</i> sp./ <i>Eleocharis microcarpa</i>	<i>Limnobium spongia</i>
August 1995	<i>Ludwigia peploides</i>	<i>Ludwigia peploides</i>
	<i>Eleocharis microcarpa</i>	<i>Eleocharis microcarpa</i>
	Cyperaceae	<i>Ludwigia palustris</i>
	<i>Spirodela polyrrhiza</i> /Ludwigia palustris	<i>Sagittaria latifolia</i>
	<i>Bidens aristosa</i>	<i>Spirodela polyrrhiza</i>
September 1995	<i>Ludwigia peploides</i>	<i>Ludwigia peploides</i>
	<i>Cephalanthus occidentalis</i>	<i>Cyperus iria</i>
	<i>Cyperus iria</i>	<i>Eleocharis microcarpa</i>
	<i>Bidens aristosa</i>	<i>Cephalanthus occidentalis</i>
	<i>Eleocharis microcarpa</i>	<i>Sphenoclea zeylanica</i>
October 1995	<i>Cyperus erythrorhizos</i>	<i>Cyperus erythrorhizos</i>
	<i>Cephalanthus occidentalis</i>	<i>Cephalanthus occidentalis</i>
	<i>Triadenum walteri</i>	<i>Eleocharis microcarpa</i>
	<i>Eleocharis microcarpa</i> /Eclipta prostrata	<i>Fimbristylus miliaceae</i> /T. walteri
	<i>Bidens aristosa</i>	<i>Leptochloa fascicularis</i>
June 1996	<i>Wolffia</i> sp.	<i>Utricularia inflata</i>
	<i>Spirodela polyrrhiza</i>	<i>Wolffia</i> sp.
	<i>Utricularia inflata</i>	<i>Spirodela polyrrhiza</i>
	<i>Ludwigia peploides</i>	<i>Ludwigia peploides</i>
	<i>Limnobium spongia</i> /Azolla caroliniana	<i>Potamogeton</i> sp.

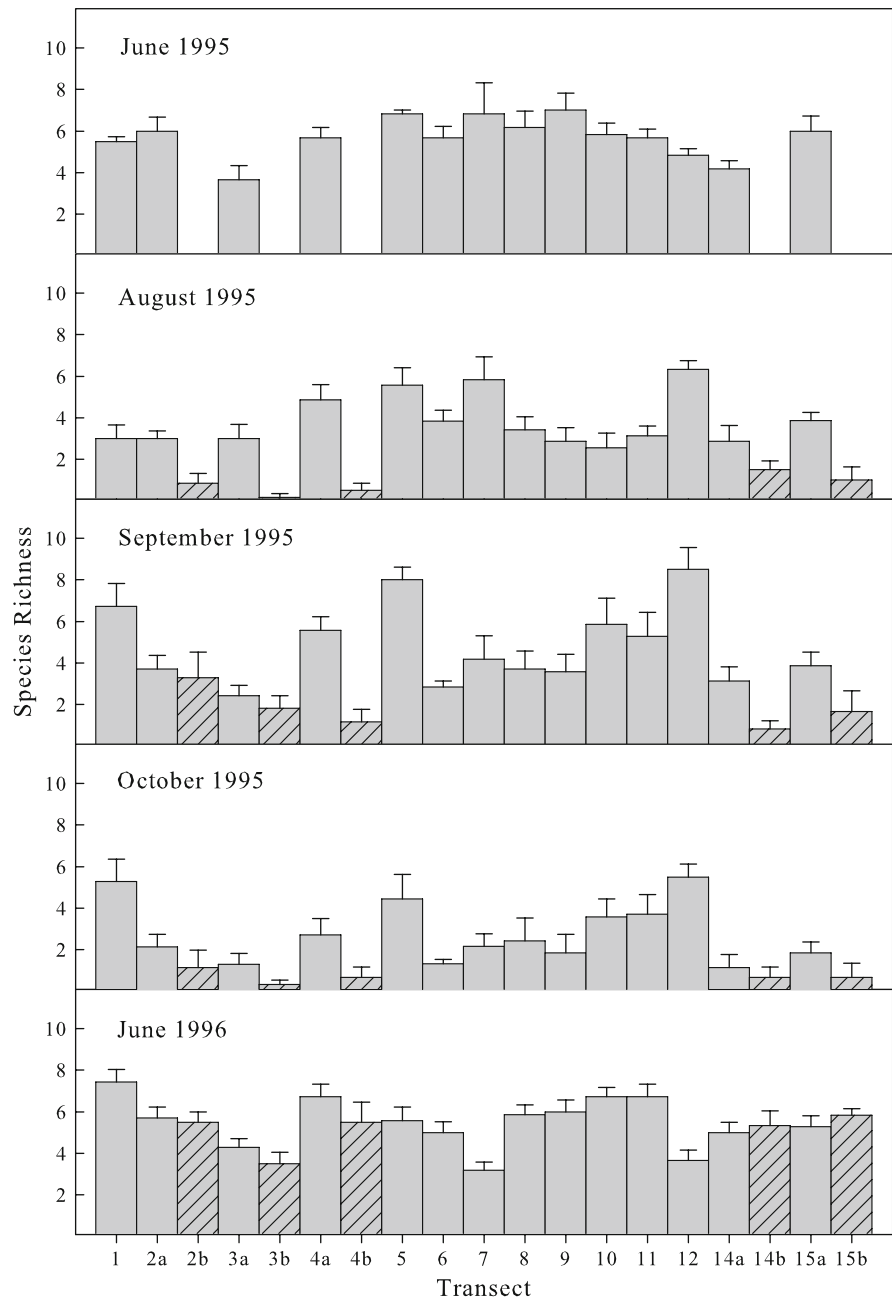
elevations; this pattern was also evident from September to October with the exception of a single transect where cover decreased at both elevations. *Cyperus* cover increased at both time intervals, to a greater magnitude at low compared to high elevations.

When undisturbed transects were pooled, elevation did not affect vegetation response in June 1995 ( $P = 0.2869$ ) or June 1996 ( $P = 0.3595$ ). Repeated measures analysis of data collected during the drawdown indicated a significant elevation effect ( $P = 0.0225$ ) across time for the undisturbed transects. Species richness and total cover increased from August to September, to a greater extent in low compared to high elevations. *Cyperus* cover increased from August to September at low elevation but decreased at high elevation. Elevation did not affect vegetation response when disturbed transects were pooled, either during the drawdown ( $P = 0.3573$ ) or in June 1996 ( $P = 0.5620$ ).

### Seed bank

A total of 39 species that germinated in the two seed bank studies was identified (Table 5), 17 species in the June samples and 33 in the October samples; one species remained unidentified in both studies. Thirteen species found in the seed bank studies were not present during field sampling at any time. The species that germinated in the most quadrats at both sampling times was *Cyperus erythrorhizos* (Table 6). Mean species richness was  $4.6 \pm 0.4$  ( $n = 28$ ) in June and  $5.5 \pm 0.3$  ( $n = 38$ ) in October. Elevation had no effect on seed bank species richness at either time ( $P = 0.2092$  in June,  $P = 0.2284$  in October). Considering undisturbed transects only, a two sample  $t$ -test indicated no difference ( $P = 0.083$ ) in mean species richness in June compared to October. Comparison of the five paired transects with soil disturbance indicated no effect ( $P = 0.5763$ ) of the disturbance on mean species richness ( $5.8 \pm 0.6$  in

**Fig. 3** Total species richness (mean  $\pm$  SE) by transect at five times. The letter “a” indicates the undisturbed transect for the five paired transects; disturbed transects are indicated by the letter “b” and by hatching



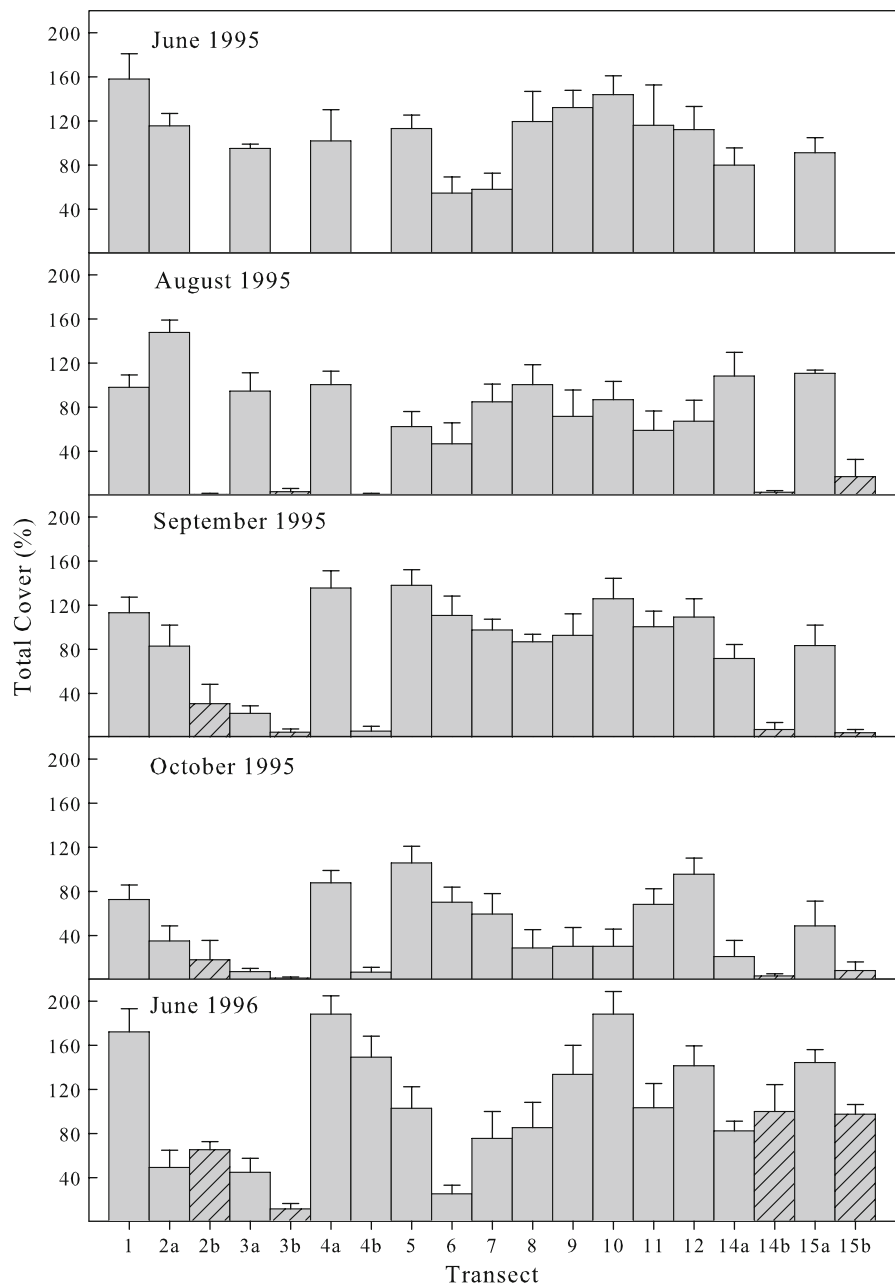
disturbed transects,  $5.5 \pm 0.4$  in undisturbed transects;  $n = 10$ ). Disturbance within elevation also did not affect species richness ( $P = 0.6213$  at low elevation,  $P = 0.4557$  at high elevation;  $n = 5$ ). Comparisons between standing vegetation and germinating seeds indicated that standing vegetation richness exceeded that of the seed bank in June at low elevation only, but that seed bank richness exceeded

standing vegetation at both elevations in October (Table 7).

#### Disturbance effects and soil characteristics

Disturbance, which consisted of scraping the soil surface with a bulldozer, significantly affected species richness and total cover during the pool

**Fig. 4** Total vegetation cover (mean  $\pm$  SE) by transect at five times. Disturbed transects are indicated by hatching. The letter “a” indicates the undisturbed transect for the five paired transects; disturbed transects are indicated by the letter “b” and by hatching. Cover can exceed 100% because various species may be present in different strata

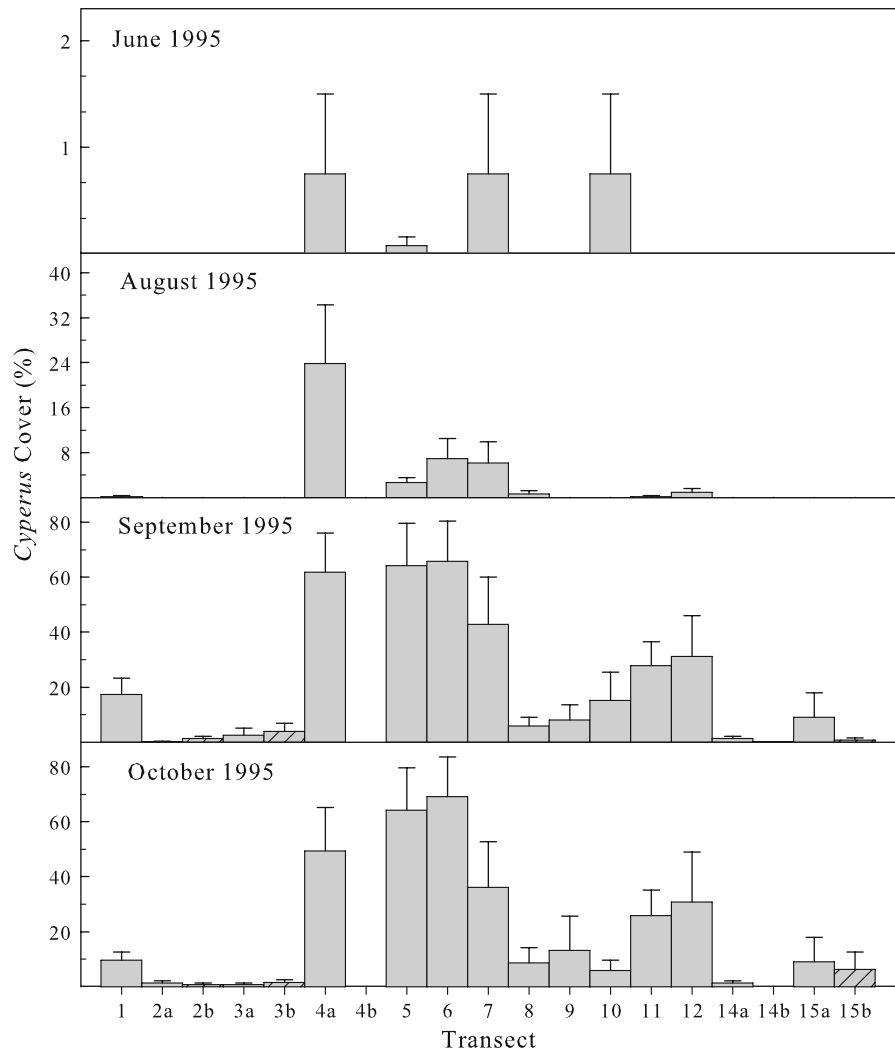


drawdown. Soil disturbance decreased species richness at all three times and decreased total cover in August and September (Table 8). Total cover was greater at undisturbed transects in both elevation classes in August and September; in October, however, cover was greater in undisturbed transects only at low elevations (Fig. 6). A similar pattern for species richness (i.e., greater values in undisturbed compared to disturbed transects) was found (data not

shown). Disturbance did not significantly affect *Cyperus* cover at any time. In June 1996, no effect of disturbance on species richness ( $P = 0.4658$ ) or total cover ( $P = 0.2874$ ) was identified.

Organic matter content in soils along the pool margin in June 1995 ranged from  $3.57 \pm 0.48$  to  $6.32 \pm 0.65\%$ , and varied by transect ( $P < 0.001$ ) and elevation class ( $P < 0.001$ ). For six transects that had a significant elevation effect, organic matter

**Fig. 5** *Cyperus* cover (mean  $\pm$  SE; includes *Cyperus erythrorhizos*, *Cyperus iria*, and Cyperaceae) by transect at five times. The letter “a” indicates the undisturbed transect for the five paired transects; disturbed transects are indicated by the letter “b” and by hatching. Note different scales on y axis



**Table 3** Overall vegetation response (mean  $\pm$  SE) at five sampling times on undisturbed (Undisturb,  $n = 84$  June 1995;  $n = 95$  all other times) and four sampling times on disturbed (Disturb,  $n = 31$ ) sampling quadrats

Time	Species richness		Total cover (%)		Cyperus cover (%)	
	Undisturb	Disturb	Undisturb	Disturb	Undisturb	Disturb
June 1995	5.7 $\pm$ 0.2		106.4 $\pm$ 5.8		0.2 $\pm$ 0.1	
August 1995	3.8 $\pm$ 0.2	0.8 $\pm$ 0.2	89.0 $\pm$ 4.8	4.8 $\pm$ 3.0	2.9 $\pm$ 1.0	0.0 $\pm$ 0.0
September 1995	4.8 $\pm$ 0.3	1.8 $\pm$ 0.4	97.5 $\pm$ 4.8	11.1 $\pm$ 4.5	24.5 $\pm$ 3.5	1.2 $\pm$ 0.6
October 1995	2.8 $\pm$ 0.3	0.7 $\pm$ 0.3	53.6 $\pm$ 4.8	7.8 $\pm$ 4.3	22.5 $\pm$ 3.5	1.7 $\pm$ 1.2
June 1996	5.6 $\pm$ 0.2	5.0 $\pm$ 0.3	110.6 $\pm$ 7.0	81.9 $\pm$ 10.5	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0

at high elevation was greater than that at low elevation. In October, when just a single quadrat was sampled, organic matter did not differ among transects ( $P = 0.07$ ). Soil disturbance significantly

( $P = 0.0397$ ;  $n = 5$ ) affected organic matter content, which was greater at undisturbed ( $7.57 \pm 1.04\%$ ) compared to disturbed ( $4.44 \pm 0.76\%$ ) treatments. Organic matter content in October ( $7.28 \pm$

**Table 4** Results of repeated measures MANOVA ( $F$  values) of undisturbed and disturbed transects during pool drawdown, in August, September, and October 1995

Source	Undisturbed transects	Disturbed transects
Trans	1.94*	0.73
Elev (Trans)	2.44**	1.33
Time <sup>a</sup>	–	–
Time*Trans	1.03	–
Time*Elev (Trans)	2.67**	0.74

Abbreviations are *Trans*, transect and *Elev*, elevation class. Significance values are  $P < 0.05^*$  and  $P < 0.0001^{**}$

<sup>a</sup> Insufficient degrees of freedom to estimate effect

0.60%) was greater than that in June ( $4.30 \pm 0.30\%$ ;  $n = 14$ ;  $P = 0.0014$ ) on undisturbed transects (quadrat 4 data only). Texture analyses indicated a predominance of clay in the upper 15-cm layer of pool soils; mean values ( $n = 14$ ) were  $14.04 \pm 0.23\%$  for sand,  $25.01 \pm 4.34\%$  for silt, and  $60.94 \pm 4.43\%$  for clay.

## Discussion

The 0.3 m drawdown of the pool exposed sediment that had been continuously flooded for almost 10 years. Total vegetation cover of emergent species was relatively high 4 weeks following the initiation of the drawdown (on 1 August 1995) (Fig. 4). This is consistent with other studies that have documented the importance of persistent seed banks in contributing to the development of plant communities following freshwater lake drawdowns (Keddy and Reznicek 1982; ter Heerdt and Drost 1994; DeBerry and Perry 2005) as well as drawdowns of emergent wetlands (Smith and Kadlec 1983; Welling et al. 1988). Plant species dominance in the drawdown zone shifted from the submersed and floating-leaved species that were present at normal pool stage to herbaceous emergent species; a woody species, *Cephalanthus occidentalis*, was also dominant during the drawdown. Several of the species that colonized the drawdown zone are considered good seed producers and are valuable food sources for waterfowl (Fredrickson and Taylor 1982). Abundant waterfowl food species documented within the drawdown zone included *Cyperus erythrorhizos*, *Echinochloa crus-galli*, *Fimbristylus miliacea*, *Leptochloa fascicularis*, *Bidens aristosa*, and *Panicum* sp.

In addition to the benefits to waterfowl species, Twedt et al. (1998) described the value of habitat created by reservoir drawdowns in the Mississippi Alluvial Valley to shorebirds; these authors recommended drawing down public reservoirs from July through October to provide shorebird foraging habitat during southward migration.

A regional drawdown flora was identified by DeBerry and Perry (2005) for a reservoir in Virginia. The flora consisted of species that form persistent seed banks in the substrate of reservoirs and characteristically produce small seeds on dense inflorescences; these species therefore are capable of producing viable seeds in large quantities. *Cyperus erythrorhizos*, which was dominant in the pool drawdown zone in our study, was part of the drawdown flora described by DeBerry and Perry (2005). Seeds of *Cyperus erythrorhizos* have been shown to be persistent under flooded conditions and are able to germinate quickly when water recedes (Baskin et al. 1993).

The number, frequency and cover of woody species increased as a result of the drawdown. Most of the woody plants identified in September and October were small seedlings of *Cephalanthus occidentalis*, *Planera aquatica* and *Taxodium distichum*. The drop in woody species richness and frequency measured in October compared to September was probably due to grazing by small mammals, including nutria (*Myocastor coypus*), which were abundant in the study area. Because only one measurement was made at base pool stage (i.e., 19.8 m msl) following the drawdown, it is not known if the increase in woody species cover persisted. It is probable, however, that continued flooding was stressful to young seedlings and may have led to their death. Studies of newly-germinated seedlings (less than 2 weeks of age) of the flood-tolerant species *Taxodium distichum* displayed substantial mortality after 45 days of submergence, but year-old seedlings were able to survive up to 5 months (Souther and Shaffer 2000). In a study on vegetation succession in Ohio, woody plant encroachment was not a problem after seven consecutive years of July to September drawdowns in marsh habitat (Meeks 1969). In warmer climates, however, more rapid growth of woody species may become an issue of concern if the spread of these species is not desired. For example, annual summer drawdowns at Catahoula Lake in central Louisiana

**Table 5** Species that germinated in soil collected at Felsenthal National Wildlife Refuge in June and October 1995, and the presence of those species in the standing vegetation at any of the five sampling events

Species	June 1995	October 1995	Standing vegetation
<i>Ammannia coccinea</i> Rottb.	x	x	x
<i>Bacopa egensis</i> (Poepp.) Pennell	x		x
<i>Bacopa rotundifolia</i> (Michx.) Wettst	x		x
<i>Bidens aristosa</i> (Michx.) Britt.		x	x
<i>Cephalanthus occidentalis</i> L.		x	x
<i>Chamaesyce humistrata</i> (Englem.) Small		x	
<i>Coreopsis</i> sp.		x	
<i>Cyperus erythrorhizos</i> Muhl.	x	x	x
<i>Cyperus esculentus</i> L.		x	
<i>Cyperus iria</i> L.		x	x
<i>Cyperus</i> sp.		x	
<i>Echinochloa crus-galli</i> (L.) Beauv.		x	x
<i>Eleocharis microcarpa</i> Torr.	x	x	x
<i>Eleocharis obtusa</i> (Willd.) J. A. Schultes		x	x
<i>Eclipta prostrata</i> (L.) L.		x	x
<i>Eupatorium capillifolium</i> (Lam.) Small		x	
<i>Fimbristylis autumnalis</i> (L.) Roemer & J. A. Shultes.		x	
<i>Fimbristylus miliacea</i> (L.) Vahl	x	x	x
<i>Gratiola virginiana</i> L.		x	
<i>Heteranthera reniformis</i> Ruiz & Pavon	x		x
<i>Leersia virginica</i> Willd.		x	
<i>Lindernia dubia</i> v. <i>anagallidea</i> (Michx) Cooperrider		x	
<i>Lindernia dubia</i> (L.) Pennell	x		x
<i>Limnium spongia</i> (Bosc) L. C. Rich. ex Steud.	x	x	x
<i>Ludwigia decurrens</i> Walt.	x	x	x
<i>Ludwigia leptocarpa</i> (Nutt.) Hara		x	x
<i>Ludwigia palustris</i> (L.) Ell.	x	x	x
<i>Ludwigia peploides</i> (Kunth) Raven	x	x	x
<i>Ludwigia sphaerocarpa</i> Ell.		x	x
<i>Panicum virgatum</i> L.		x	
Poaceae	x	x	x
<i>Ptilimnium capillaceum</i> (Michx) Raf.		x	
<i>Sagittaria latifolia</i> Willd.	x		x
<i>Salix nigra</i> Marsh.		x	
<i>Solidago</i> sp.		x	
<i>Spirodela polyrrhiza</i> (L.) Schleid.	x	x	x
<i>Sphenoclea zeylanica</i> Gaertn.		x	x
Bryophytes:			
<i>Riccia</i> sp.	x	x	x
<i>Ricciocarpos</i> sp.	x		x

have resulted in the encroachment of *Cephalanthus occidentalis* and *Forestiera acuminata* into the drawdown zone over the past several decades

(T. Michot, oral commun.); apparently, some seedlings were able to grow tall enough to remain above water level during normal lake levels. At Lake

**Table 6** The ten most common species that germinated in soil samples collected in June and October 1995 at Felsenthal National Wildlife Refuge

Month	Species	Frequency
June 1995	<i>Cyperus erythrorhizos</i>	0.82
	<i>Ludwigia peploides</i>	0.50
	<i>Lindernia dubia</i>	0.46
	Poaceae	0.43
	<i>Spirodela polyrrhiza</i>	0.43
	<i>Bacopa egensis</i>	0.36
	<i>Ricciocarpus</i> sp.	0.36
	<i>Riccia</i> sp.	0.25
	<i>Limnobium spongia</i>	0.21
	<i>Ludwigia decurrens</i>	0.14
October 1995	<i>Cyperus erythrorhizos</i>	1.00
	<i>Lindernia dubia</i> v. <i>anagallidea</i>	0.50
	<i>Ludwigia peploides</i>	0.46
	<i>Ludwigia palustris</i>	0.29
	<i>Ammania coccinea</i>	0.25
	<i>Ludwigia leptocarpa</i>	0.25
	<i>Eleocharis obtusa</i>	0.21
	Poaceae	0.21
	<i>Eleocharis microcarpa</i>	0.18
	<i>Bidens aristosa</i>	0.14

Frequency indicates the portion of total soil samples ( $n = 28$ ) in undisturbed transects in which the species germinated

**Table 7** Species richness (mean  $\pm$  SE,  $n = 14$ ) of seed bank samples and of standing vegetation in high and low elevation quadrats; soil for seed bank studies was collected outside the quadrats where vegetation was measured

Time	Low elevation		High elevation	
	Vegetation	Seed bank	Vegetation	Seed bank
June	6.1 $\pm$ 0.4 <sup>a</sup>	4.1 $\pm$ 0.4 <sup>b</sup>	5.2 $\pm$ 0.5	5.1 $\pm$ 0.6
October	3.5 $\pm$ 0.8 <sup>a</sup>	5.1 $\pm$ 0.5 <sup>b</sup>	3.2 $\pm$ 0.6 <sup>a</sup>	6.0 $\pm$ 0.5 <sup>b</sup>

Significant differences between standing vegetation and seed bank within elevation class by time are indicated by different letters

Chicot, also in central Louisiana, *Taxodium distichum* seedlings were able to establish on exposed sediments when the drawdown extended over 18 months and included two consecutive growing seasons (Keeland and Conner 1999).

The effects of transect and elevation on vegetation response were complex. Although response varied

with transect among those transects that were not subjected to soil disturbance, there was no consistent pattern in groupings related to direction of location along the pool margin (north, south, east, or west) or to soil characteristics. Elevation significantly affected vegetation at some transects during the drawdown, and those effects were somewhat consistent. Values reflecting vegetation response were often greater at low elevation than those at high elevation. When a response increased over time at both elevations, the magnitude of the increase was greater at low compared to high elevation. When a response decreased over time at both elevations, as did species richness from September to October on three transects, the relationship between elevations was variable. These responses may be related to species phenology and/or weather conditions during the study. The decrease in total cover on undisturbed transects in October probably reflects seasonal senescence of some species. In contrast, cover of annual *Cyperus* species, which can flower late in the growing season, remained fairly constant in September and October. The summer of 1995 was unusually dry in southern Arkansas with total precipitation of 23.7 cm from June through October (Felsenthal NWR records); for comparison, the 30-year (1961–1990) mean average for this time period was 50.4 cm (Crossett Water Commission, Crossett, Arkansas). Soil moisture has been found to influence recruitment of species from the seed bank (Welling et al. 1988), and Moore and Keddy (1988) noted that minor changes in water level cause significant changes in the species of lakeshore plants that germinate. It is likely that low elevation locations at the pool had sufficient moisture for seed germination and vigorous plant growth for the first several weeks of drawdown. During late summer to fall, however, the cumulative effect of the drought may have led to a dieback in vegetation. A possible explanation for the greater decrease in species richness observed at low compared to high elevation is that some species present at low elevation were more susceptible to reduced soil moisture in late summer than were species at high elevations, so the decrease in richness would be more dramatic at the low elevation sites. We also noted heavy insect (beetle) herbivory in September 1995; *Ludwigia peploides* was the species affected to the greatest degree and was often grazed to the extent where only stems remained. Because of structural

**Table 8** Vegetation response (mean  $\pm$  SE) in five undisturbed (Undisturb) and five disturbed (Disturb) transects

Month	Species richness		Total cover (%)		<i>Cyperus</i> cover (%)	
	Undisturb	Disturb	Undisturb	Disturb	Undisturb	Disturb
August	3.5 $\pm$ 0.3 <sup>a</sup>	0.8 $\pm$ 0.2 <sup>b</sup>	112.1 $\pm$ 6.8 <sup>a</sup>	4.8 $\pm$ 3.0 <sup>b</sup>	4.8 $\pm$ 2.6	0.0 $\pm$ 0.0
September	3.7 $\pm$ 0.3 <sup>a</sup>	1.8 $\pm$ 0.4 <sup>b</sup>	79.0 $\pm$ 8.9 <sup>a</sup>	11.1 $\pm$ 4.5 <sup>b</sup>	15.0 $\pm$ 5.2	1.2 $\pm$ 0.6
October	1.8 $\pm$ 0.3 <sup>a</sup>	0.7 $\pm$ 0.3 <sup>b</sup>	39.9 $\pm$ 7.6	7.8 $\pm$ 4.3	12.3 $\pm$ 4.7	1.7 $\pm$ 1.2
June	5.4 $\pm$ 0.3	5.1 $\pm$ 0.3	101.7 $\pm$ 11.1	84.6 $\pm$ 10.4	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0

Data were collected in August, September and October 1995 and June 1996

Significant differences ( $P < 0.05$ ) between undisturbed and disturbed transects from ANOVA are indicated by different letters

similarity between dominant species in June 1995 and June 1996, is unlikely that the species composition shift affected plant community function.

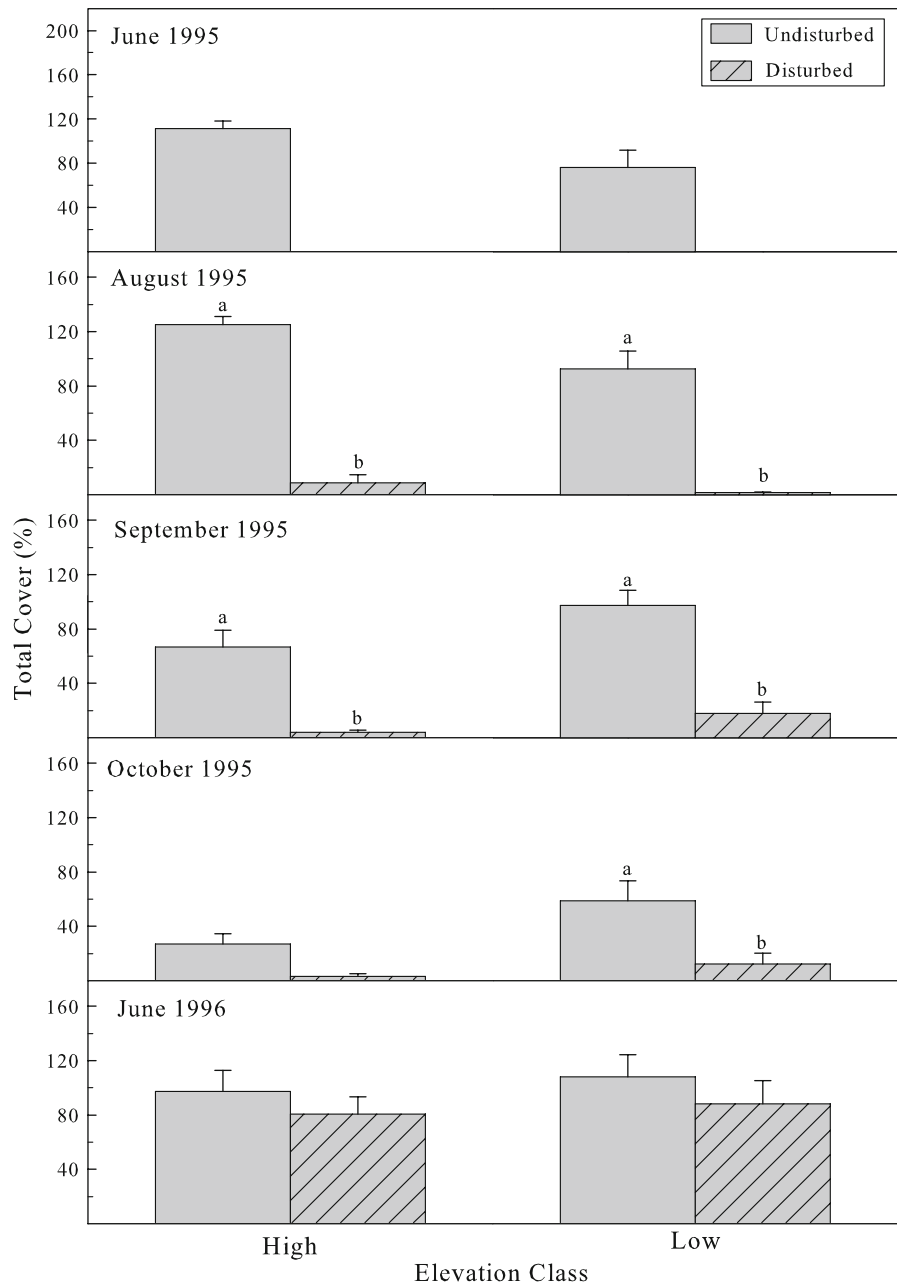
Analyses of the seed bank data were problematic because different soil volumes were collected in June and October, which likely affected the total number of seeds present. Although data on species abundance (i.e., cover class at two time intervals) were collected for each seed bank study, only data on species richness were analyzed; we do not believe that the sample size difference invalidated analyses that included this variable. Species richness per quadrat was not different between the two times, but species composition did vary. There were 22 species that germinated in October samples that were not present in June samples, and six that germinated in June but not October samples. This variation is probably related to three factors: (1) species variation in timing of flowering and seed maturation, (2) inherent variability in seed longevity and seed dispersal, especially in rare species, and (3) the effect of prolonged flooding on seed recruitment.

Our seed bank results are consistent with those of Leeds et al. (2002), who found that more species germinated in Florida Everglades soils collected in October than in soils collected in May. This variation was attributed to a July peak in seed maturity and dispersal (Leeds et al. 2002). Seed longevity varies widely among plants, ranging from less than a year to several decades (Baskin and Baskin 1998). Many of the woody species present in bottomland hardwood forests produce short-lived seeds that are dispersed by water (Schneider and Sharitz 1986; Middleton 2000). Herbaceous species are well represented in the seed banks of forested systems (Leck 1989; Middleton 2003); in general, the mean longevity of seeds of wetland species exceeds that of woody species by

about three times (Thompson et al. 1998). Results from our seed emergence studies indicate the predominance of herbaceous species in the seed bank at the pool. While seed persistence is primarily a species trait, it can be modified by environmental conditions (Fenner and Thompson 2005). A reduction in seed species richness or density in wetland seed banks under prolonged flooding has been noted in several studies (e.g., Keddy and Reznicek 1982; Smith and Kadlec 1983; Schneider and Sharitz 1986; Leck 1989; Poiani and Johnson 1989; Petersen and Baldwin 2004). This reduction may be due to lower incorporation of seeds in standing water (Schneider and Sharitz 1986); however, the anoxic conditions found in flooded soils reduces seed deterioration (Leck 1989) and therefore can increase seed longevity. The higher species richness in standing vegetation versus that of germinating seeds that we observed in June is consistent with a study by Bossuyt et al. (2007), who examined a drained lake bed in Belgium. We can not be confident that this difference is real; as noted by Bossuyt et al. (2007), it may be an artifact of the difference in sample size (i.e., quadrat size was several times larger than the soil core). Higher species richness in the seed bank compared to standing vegetation, which we identified in October, is the more common relationship reported for wetlands (Smith and Kadlec 1983; Schneider and Sharitz 1986; Wilson et al. 1993).

Soil disturbance decreased species richness and total vegetation cover during the drawdown. Although soil disking and tilling are recommended as a management technique to facilitate seed germination (Fredrickson and Reid 1988; Gray et al. 1999), disking at the pool margin was logistically difficult due to the abundant woody debris. The use of a bulldozer to remove the woody debris scraped away

**Fig. 6** Total vegetation cover by elevation class (mean  $\pm$  SE,  $n = 5$ ) on undisturbed and disturbed transects at five sampling times (disturbed transects not sampled in June 1995). Elevation classes are: H (high):  $\geq 15$  cm and L (low):  $< 15$  cm. Significant differences between means are indicated by different letters



topsoil, thereby removing much of the available seed bank. It is likely that low summer rainfall levels contributed to low germination of seeds that were recruited onto disturbed transects. The soils of the pool margin were predominantly clay with low organic matter content. Although there was no consistent trend in vegetation by elevation class in June 1995, the higher organic matter content found for some transects at high compared to low elevation

may be related to greater production by plants across the growing season at high elevation (i.e., water less than 15-cm deep) over the 10-year flooding period. Organic matter content at the water edge may have been influenced by the tendency for floating debris to accumulate along the shoreline. The increase in organic matter from June to October is counterintuitive. Although the aerobic conditions and higher soil temperatures during the drawdown would be

expected to increase decomposition and therefore reduce organic matter content, the low rainfall and extremely dry conditions during the study would impede decomposition. In addition, difference in litter quality exists between the two times. The submersed and floating-leaved species of June are more easily consumed by microbial decomposers than the sedge and woody species that dominated in October, which have higher concentrations of recalcitrant materials such as lignin and cellulose (Lockaby et al. 1996). The lower organic matter on disturbed compared to undisturbed sites was due to the fact that application of the soil disturbance removed the top few centimeters of soil.

In summary, the 0.3-m drawdown at the pool resulted in an increase in both emergent and woody vegetation cover within the area of exposed soil and was accompanied by an increase in cover of waterfowl food species. Total vegetation cover was generally high in undisturbed transects during the drawdown, and species richness and cover were often higher at low compared to high elevation. Seed bank studies indicated that seeds of some plants, including valuable waterfowl food species, persisted during the 10-year period the pool was flooded and that the diversity of the seed bank increased during the drawdown. The application of soil disturbance, which removed the upper layers of soil, decreased species richness and cover by removing the existing seed bank; these negative effects were probably intensified by the extremely dry weather conditions during the study. Pool vegetation in early summer following the drawdown was structurally similar to that of vegetation prior to the drawdown. Future drawdown events are likely to follow the same trajectory, increasing food quality and quantity for waterfowl species. If management goals include maintenance of open water conditions, permanent encroachment of woody vegetation into the drawdown zone is unlikely if drawdowns are scheduled on a cycle that subject young seedlings to flooding stress in the subsequent growing season. Studies in other geographic regions would indicate if the information documented by our study on basic plant community response to temporary water level drawdowns in reservoirs is applicable beyond the southeastern United States.

**Acknowledgments** We appreciate the assistance provided by the staff at Felsenthal NWR throughout the study. Most notably,

the logistical support and help provided by R. Ellis in locating sampling sites, collecting data, and identifying plant species were essential. We thank D. Johnson for completing statistical analyses, J. Biagas for help with field data collection and graphics preparation, and C. Boudreaux for graphics assistance. Historical data on water levels at Felsenthal lock and dam were provided by B. Keeland. Comments on the manuscript from S. Faulkner, T. Michot, R. Dale, B. Middleton, J. Waide, and two anonymous reviewers are greatly appreciated. The use of trade, product or firm names does not constitute endorsement or recommendation for use by the US Government.

## References

- Baskin CC, Baskin JM (1998) Seeds—ecology, biogeography and evolution of dormancy and germination. Academic Press, San Diego
- Baskin CC, Baskin JM, Chester EW (1993) Seed germination ecophysiology of four summer annual mudflat species of Cyperaceae. *Aquat Bot* 45:41–52. doi:[10.1016/0304-3770\(93\)90051-W](https://doi.org/10.1016/0304-3770(93)90051-W)
- Bonham CD (1989) Measurements for terrestrial vegetation. John Wiley and Sons, New York
- Bossuyt B, van Wichelen J, Hoffman M (2007) Predicting future community composition from random soil seed bank sampling—evidence from a drained lake bottom. *J Veg Sci* 18:443–450. doi:[10.1658/1100-9233\(2007\)18\[443:PFCCFR\]2.0.CO;2](https://doi.org/10.1658/1100-9233(2007)18[443:PFCCFR]2.0.CO;2)
- Broadfoot WM (1958) Reaction of hardwood timber to shallow-water impoundments. Mississippi State University Agricultural Experiment Station Information Sheet 595, Mississippi State University, Stoneville
- Broadfoot WM (1967) Shallow-water impoundment increases soil moisture and growth of hardwoods. *Soil Sci Soc Am Proc* 31:562–564
- Brock SC, Arner DH, Steffen DE (1994) Seed yields of four moist-soil plants on Noxubee National Wildlife Refuge. *Proc Ann Conf Southeast Assoc Fish Wild Agencies* 48:38–47
- Casanova MT, Brock MA (2000) How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecol* 147:237–250. doi:[10.1023/A:1009875226637](https://doi.org/10.1023/A:1009875226637)
- DeBerry DA, Perry JE (2005) A drawdown flora in Virginia. *Castanea* 70:276–286. doi:[10.2179/0008-7475\(2005\)070\[0276:ADFIV\]2.0.CO;2](https://doi.org/10.2179/0008-7475(2005)070[0276:ADFIV]2.0.CO;2)
- Ervin GN, Majure LC, Bried JT (2006) Influence of long-term greentree reservoir impoundment on stand structure, species composition, and hydrophytic indicators. *J Torrey Bot Soc* 133:468–481. doi:[10.3159/1095-5674\(2006\)133\[468:IOLGRI\]2.0.CO;2](https://doi.org/10.3159/1095-5674(2006)133[468:IOLGRI]2.0.CO;2)
- Fenner M, Thompson K (2005) The ecology of seeds. Cambridge University Press, Cambridge
- Fredrickson LH (1991) Waterfowl management handbook. Fish and Wildlife Leaflet 13.4.6—Strategies for water level manipulations in moist-soil systems. US Fish and Wildlife Service, Washington, DC
- Fredrickson LH (2005) Greentree reservoir management—implications of historic practices and contemporary

- considerations to maintain habitat values. In: Fredrickson LH, King SL, Kaminski RM (eds) Ecology and management of bottomland hardwood systems—the state of our understanding. Gaylord Memorial Laboratory special publication no. 10. University of Missouri, Columbia, pp 479–486
- Fredrickson LH, Batema DL (1992) Greentree reservoir management handbook. Wetland management series no. 1. Gaylord Memorial Laboratory. University of Missouri, Columbia
- Fredrickson LH, Reid FA (1988) Waterfowl management handbook. Fish and Wildlife Leaflet 13.4.9—Preliminary considerations for manipulating vegetation. US Fish and Wildlife Service, Washington, DC
- Fredrickson LH, Taylor TS (1982) Management of seasonally flooded impoundments for wildlife. US Fish and Wildlife Service Resource Publication 148, Washington, DC
- Gray MJ, Kaminski RM (2005) Effect of continuous flooding versus periodic winter flooding on survival of oak seedlings in Mississippi greentree reservoirs. In: Fredrickson LH, King SL, Kaminski RM (eds) Ecology and management of bottomland hardwood systems—the state of our understanding. Gaylord Memorial Laboratory special publication no. 10. University of Missouri, Columbia, pp 487–493
- Gray MJ, Kaminski RM, Weerakkody G, Leopold BD, Jensen KC (1999) Aquatic invertebrate and plant responses following mechanical manipulations of moist-soil habitat. *Wildl Soc Bull* 27:770–779
- Keddy PA, Reznicek AA (1982) The role of seed banks in the persistence of Ontario's coastal plain flora. *Am J Bot* 69:13–22. doi:[10.2307/2442827](https://doi.org/10.2307/2442827)
- Keeland BD, Conner WH (1999) Natural regeneration and growth of *Taxodium distichum* (L.). Rich in lake Chicot, Louisiana, after 44 years of flooding. *Wetlands* 19:149–155
- King SL, Allen JA (1996) Plant succession and greentree reservoir management—implications for management and restoration of bottomland hardwood wetlands. *Wetlands* 16:503–511
- King SL, Allen JA, McCoy JW (1998) Long-term effects of a lock and dam and greentree reservoir management on a bottomland hardwood forest. *For Ecol Manage* 112:213–226
- Leck MA (1989) Wetland seed banks. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press, San Diego, pp 283–304
- Leck MA, Simpson RL (1995) Ten-year seed bank and vegetation dynamics of a tidal freshwater marsh. *Am J Bot* 82:1547–1557. doi:[10.2307/2446183](https://doi.org/10.2307/2446183)
- Leeds JA, Smith SM, Garrett PB (2002) Seedbanks and their potential role in the vegetation dynamics of a northern Everglades marsh. *Fla Sci* 65:16–34
- Lockaby BG, Wheat RS, Clawson RG (1996) Influence of hydroperiod on litter conversion to soil organic matter in a floodplain forest. *Soil Sci Soc Am J* 60:1989–1993
- Malecki RA, Lassoie JR, Rieger E, Seamans T (1983) Effects of long-term artificial flooding on a northern bottomland hardwood community. *For Sci* 29:535–544
- Meeks RL (1969) The effect of drawdown date on wetland plant succession. *J Wildl Manage* 33:817–821. doi:[10.2307/3799312](https://doi.org/10.2307/3799312)
- Merz RW, Brakhage GK (1964) The management of pin oak in a duck shooting area. *J Wildl Manage* 28:233–239. doi:[10.2307/3798082](https://doi.org/10.2307/3798082)
- Middleton B (2000) Hydrochory, seed banks, and regeneration dynamics along the landscape boundaries of a forested wetland. *Plant Ecol* 146:169–184. doi:[10.1023/A:1009871404477](https://doi.org/10.1023/A:1009871404477)
- Middleton B (2003) Soil seed banks and the potential restoration of forested wetlands after farming. *J Appl Ecol* 40:1025–1034. doi:[10.1111/j.1365-2664.2003.00866.x](https://doi.org/10.1111/j.1365-2664.2003.00866.x)
- Moore DRJ, Keddy PA (1988) Effects of a water-depth gradient on the germination of lakeshore plants. *Can J Bot* 66:548–552
- Petersen JE, Baldwin AH (2004) Seedling emergence from seed banks of tidal freshwater wetlands: response to inundation and sedimentation. *Aquat Bot* 78:243–254. doi:[10.1016/j.aquabot.2003.10.005](https://doi.org/10.1016/j.aquabot.2003.10.005)
- Poiani KA, Johnson WC (1988) Evaluation of the emergence method in estimating seed bank composition of prairie wetlands. *Aquat Bot* 32:91–97. doi:[10.1016/0304-3770\(88\)90090-3](https://doi.org/10.1016/0304-3770(88)90090-3)
- Poiani KA, Johnson WC (1989) Effect of hydroperiod on seed-bank composition in semipermanent prairie wetlands. *Can J Bot* 67:856–864. doi:[10.1139/b89-115](https://doi.org/10.1139/b89-115)
- Reineke KJ, Kaminski RM, Moorehead DJ, Hodges JD, Nasser JR (1989) Mississippi alluvial valley. In: Smith LM, Pederson RL, Kaminski RM (eds) Habitat management for migrating and wintering waterfowl in North America. Texas Tech University Press, Lubbock, pp 203–247
- Rossell IM, Wells CL (1999) The seed banks of a southern Appalachian fen and an adjacent degraded wetland. *Wetlands* 19:365–371
- Schneider RL, Sharitz RR (1986) Seed bank dynamics in a southeastern riverine swamp. *Am J Bot* 73:1022–1030. doi:[10.2307/2444121](https://doi.org/10.2307/2444121)
- Schumacher BA, Neary AJ, Palmer CJ, Maynard DG, Pastorek L, Morrison IK, Marsh M (1995) Laboratory methods for soil and foliar analysis in long-term environmental monitoring programs. US Environmental Protection Agency Report EPA/600/R-95/077. US Environmental Protection Agency, Las Vegas
- Smith LM, Kadlec JA (1983) Seed banks and their role during drawdown of a North American marsh. *J Appl Ecol* 20:673–684. doi:[10.2307/2403534](https://doi.org/10.2307/2403534)
- Soil and Plant Analysis Council (1992) Determination of organic matter by loss-on-ignition. In Handbook on reference methods for soil analysis. Council on Soil Testing and Plant Analysis, Georgia University Station, Athens, Georgia, pp 172–174
- Souther RF, Shaffer GP (2000) The effects of submergence and light on two age classes of baldcypress (*Taxodium distichum* (L.) Richard) seedlings. *Wetlands* 20:697–706. doi:[10.1672/0277-5212\(2000\)020\[0697:TEOSAL\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2000)020[0697:TEOSAL]2.0.CO;2)
- Integrated Taxonomic Information System (2007) Integrated Taxonomic Information System. <http://www.itis.gov>. Cited 7 Nov 2007
- ter Heerdt GNJ, Drost HJ (1994) Potential for the development of marsh vegetation from the seed bank after a drawdown. *Biol Conserv* 67:1–11. doi:[10.1016/0006-3207\(94\)90002-7](https://doi.org/10.1016/0006-3207(94)90002-7)

- Thompson K, Bakker JP, Bekker RM, Hodgson JG (1998) Ecological correlates of seed persistence in soils in the north-west European flora. *J Ecol* 86:163–169. doi:[10.1046/j.1365-2745.1998.00240.x](https://doi.org/10.1046/j.1365-2745.1998.00240.x)
- Twedt DJ, Nelms CO, Rettig VE, Aycock SR (1998) Shorebird use of managed wetlands in the Mississippi alluvial valley. *Am Midl Nat* 140:140–152. doi:[10.1674/0003-0031\(1998\)140\[0140:SUOMWI\]2.0.CO;2](https://doi.org/10.1674/0003-0031(1998)140[0140:SUOMWI]2.0.CO;2)
- van der Valk AG, Pederson RL (1989) Seed banks and the management and restoration of natural vegetation. In: Leck MA, Parker VT, Simpson RL (eds) *Ecology of soil seed banks*. Academic Press, San Diego, pp 329–346
- Welling CH, Pederson RL, van der Valk AG (1988) Temporal patterns in recruitment from the seed bank during draw-downs in a prairie wetland. *J Appl Ecol* 25:999–1007
- Wilson CH, Moore DRJ, Keddy PA (1993) Relationships of marsh seed banks to vegetation patterns along environmental gradients. *Freshw Biol* 29:361–370. doi:[10.1111/j.1365-2427.1993.tb00770.x](https://doi.org/10.1111/j.1365-2427.1993.tb00770.x)
- Young GL, Karr BL, Leopold BD, Hodges JD (1995) Effect of greentree reservoir management on Mississippi bottomland hardwoods. *Wildl Soc Bull* 23:525–531